Developmental transitions in body color in chacma baboon infants: implications to estimate age and developmental pace

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ABSTRACT

Objectives: In many primates, one of the most noticeable morphological developmental traits is the transition from natal fur and skin color to adult coloration. Studying the chronology and average age at such color transitions can be an easy and non-invasive method to (i) estimate the

age of infants whose dates of birth were not observed, and (ii) detect inter-individual differences in the pace of development for infants with known birth dates.

Materials and Methods: Using a combination of photographs and field observations from 73 infant chacma baboons (*Papio ursinus*) of known ages, we (1) scored the skin color of six different body parts from pink to grey, as well as the color of the fur from black to grey, (2) validated our method of age estimation using photographic and field observations on an independent subset of 22 infants with known date of birth, and (3) investigated ecological, social and individual determinants of age-related variation in skin and fur color.

Results: Our results show that transitions in skin color can be used to age infant chacma baboons less than seven months old with accuracy (median number of days between actual and estimated age = 10, range=0-86). We also reveal that food availability during the mother's pregnancy, but not during lactation, affects infant color-for-age and therefore acts as a predictor of developmental pace.

Discussion: This study highlights the potential of monitoring within- and between-infant variation in color to estimate age when age is unknown, and developmental pace when age is known.

***Keywords**: ageing method, primate, inter-individual variation, food availability*

INTRODUCTION

The relationship between age and physical maturation has been a major topic of interest in behavioral and evolutionary ecology. Across species, different developmental paces shed light on between-species life-history variations (Sibly, Grady, Venditti, & Brown, 2014). For example, primates, including humans, have longer periods of lactation, associated with slower postnatal growth and smaller litter size compared to other mammals of similar sizes (Dufour &

Sauther, 2002). Across populations and individuals of a same species, variation in infant developmental pace can have important fitness consequences on later survival and future reproduction (Lindström, 1999) as well as on maternal reproductive success, via a trade-off balancing investment in current versus future progeny (Lee, Majluf, & Gordon, 1991; Maestripieri, 2002; Trivers, 1972).

Developmental pace may vary in relation to various environmental, social, maternal and individual traits. Specifically, and as for all mammals, the quantity and quality of milk represent a primary influence on infant growth trajectory (Lee, 1996). For example, a positive impact of exclusive breastfeeding in the first 3-5 months of life on growth rates is observed among children in Bangladesh (Arifeen, Black, Caul, Antelman, & Baqui, 2001). In non-human primates, food availability between conception and weaning is an important source of variation in developmental pace, which is likely mediated by maternal condition for young infants who do not yet feed independently (Lee, 1996). As a result, the seasonal timing of birth, as well as maternal traits that may affect the nutritional status of mothers, may affect growth and development (Lee, 1996; Lummaa, 2003; Vandeleest & Capitanio, 2012). For example, in hierarchical societies, dominant females often have a better access to food, which may lead to higher reproductive rates and faster offspring development (Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011). Individual traits, like infant sex, may also impact the developmental pace of sexually dimorphic primates (Lonsdorf, 2017). Finally, selective pressures such as predation risk (Coslovsky & Richner, 2011; Fontaine & Martin, 2006), infanticide risk (Bădescu et al., 2016) or group size (Borries, Larney, Lu, Ossi, & Koenig, 2008) may further impact developmental trajectories, depending on the species considered.

In more than 30% of primate species, one of the most noticeable and widespread morphological developmental traits is the transition from natal fur and skin color to adult coloration (Ross & Regan, 2000; Treves, 1997). Neonatal fur coloration may have evolved to

promote allomaternal care, infant attraction and protection by other group members, or in response to infanticide risk (Ross & Regan, 2000; Treves, 1997). Even if the ultimate function of neonatal fur color remains unclear (Hrdy, 1976; Treves, 1997), careful monitoring of such developmental transitions at the individual level could have at least two important applications. First, if the age at which such transitions occur does not vary excessively across individuals, it can be an easy and non-invasive method to estimate individual ages in transitional infants for whom the date of birth is unknown (Altmann & Altmann, 1981). Such a method relies on the detailed description of age-related changes in body coloration for a cohort of infants of known ages. This approach, which can be applied using observational data only, has significant advantages over many other common methods, such as body weight or dental eruption patterns, which rely on invasive measurements (Hohn, 2009; Morris, 1972).

Second, for infants of known ages, inter-individual differences in the age of color transitions may reflect broader individual variation in developmental pace, if they correlate with physical growth or other indicators of behavioral development, such as social, feeding and locomotor development, or the temporal dynamics of the mother-offspring relationship (Barthold, Fichtel, & Kappeler, 2009; Treves, 1997). Few studies have investigated such correlations. Across species, the loss of natal pelage of 138 primate species is partially correlated with the temporal dynamics of mother-offspring spatial proximity, i.e. this color change begins around the period when the infant spends a considerable amount of time (25%) out of the mother's arm-reach (Treves, 1997). Within species, the transition from natal to adult fur coincides with advanced physical independence, such as independent locomotion and feeding on solid food as is the case in red-fronted lemurs (*Eulemur fulvus rufus*) (Barthold et al., 2009). In such cases, recording infant color changes at particular ages may represent one easy way to quantify individual differences in developmental pace, and an early-life indicator of weaning age, which is a crucial life history trait affecting maternal fitness.

Baboons are among the most studied of the non-human primates, but our ability to estimate infant age and our understanding of the determinants of infant developmental pace in this species are still limited. Little work has been done to estimate infant age based on color transitions since two seminal papers on yellow baboons (*Papio cynocephalus*) forty years ago (Altmann & Altmann 1981; Rasmussen 1979) - although a short preliminary study has also been published on chacma baboons (*Papio ursinus*) (Whitehead, Henzi, & Piper, 1990). These studies report that the fur and skin of infants of both species show different coloration compared to adults. When they are born, the fur is black and the exposed skin on the face, ears, hands, and feet are pink, and they gradually acquire the physical traits of adults, grey skin and dark grey fur for chacma baboons (yellow fur for yellow baboons) in their first year of life. This transition may operate following a specific chronology, with some parts of the body turning grey before others (Altmann & Altmann, 1981). However, those studies have only described the chronology of the color transitions, while the accuracy of a method based on such transitions to estimate infant ages has never been assessed.

More is known about developmental pace in baboons, but few studies have focused on the specific pace of developmental transitions in coloration. High levels of individual variation can be seen across various indicators of development including changes in fur and skin color, as well as in growth rate and behavioral development, with some infants maturing faster than others (Altmann 1980; Altmann and Alberts 2005; Altmann and Altmann 1981; Johnson 2003). Food availability in the environment is a major factor influencing individual variation in growth rate (Altmann & Alberts, 2005). The timing of the birth in the annual cycle could thus impact infant developmental pace, as seasonal variation in food availability largely occur across tropical Africa (Feng, Porporato, & Rodriguez-Iturbe, 2013). Moreover, maternal traits are also known to affect baboon infant development: yellow baboon infants of dominant females have faster growth rates and reach sexual maturity earlier than those of subordinates (Alberts &

Altmann, 1995; Altmann & Alberts, 2005; Charpentier, Tung, Altmann, & Alberts, 2008). In this same population, offspring of multiparous females are larger for their age than offspring of primiparous females (Altmann & Alberts, 2005). Overall, while the determinants of individual variation in growth trajectories have already been explored, less is known about color transitions in baboons. Examining such variation may contribute to a better understanding of processes affecting growth and physical maturation, and changes in the color of certain body parts could be used as indicators of developmental pace in baboon species.

Using the skin and fur coloration of wild infant chacma baboons, we first characterize in detail the temporal sequence of physical maturation from natal to adult-like coloration to compare the chronology of these coloration transitions with other baboon populations and species. Second, we assess the accuracy of the developed method by using these dates of coloration transitions to estimate the ages of infants, and comparing age estimates with their known birth dates. We then examine the main determinants of individual variation in body color transitions for a cohort of infants of known ages, focusing on the influence of ecological factors (food availability during pregnancy and early lactation, timing of infant birth in the annual cycle), maternal traits (rank and parity) and individual traits (sex) on the age at transitions.

Material and Methods

1 Study site

Data were taken by different field observers each year between 2005 and 2019 from three habituated groups of chacma baboons (J and L since 2005, and M, a fission of group J, since 2016) living in Tsaobis Nature Park (22°23S, 15°44’50E). Chacma baboons at the Tsaobis Baboon Project live in a semi-arid region of Namibia, on the edge of the Namib Desert. Annual rainfall is low and variable which leads to relatively low, and highly unpredictable food availability (Cowlishaw & Davies, 1997). Nonetheless, rainfall occurs most years, and peaks

between January and April, resulting in an annual food peak of variable intensity and duration from February to May. The groups were followed daily on foot from dawn to dusk, allowing observers to collect a variety of demographic, life-history, behavioral and group spatial data. Each group member was known individually through ear notches and identifying marks, and each new birth in a group was recorded. Reproductive states of adult females were recorded every day in the field, and they were classified as: (i) pregnant, where pregnancy was determined *post hoc* following infant birth, and encompassed the six months between the conceptive cycle and the birth; (ii) lactating, for the period from infant birth until the resumption of cycling; and (iii) cycling, including both swollen females (i.e., sexually receptive with a perineal swelling) and non-swollen females between two swelling phases. Groups were not followed year-round, and each year a field season of variable length was conducted (median=126 days, range: 57-240 days).

2 Ecological and individual traits

To investigate the determinants of individual variation in physical development, we considered both ecological and individual traits. We estimated food availability with the normalized difference vegetation index (NDVI). This measure has previously been used as a proxy of food availability in our population (Baniel, Cowlishaw, & Huchard, 2018) and other baboon populations (Zinner, Peí Aez, & Torkler, 2001). We extracted the mean NDVI per 16-day period on a 500 m resolution from 2004 until 2019 on the NASA website (MOD13A1 product) (Didan, Barreto Munoz, Solano, & Huete, 2015) within the home ranges of the three habituated groups. Using the GPS locations recorded every 30 minutes by the observers during daily group follows, between 2005 and 2019, we computed 100% isopleth home ranges for our three groups separately using kernel density estimates ('kernelUD' function, h set to 'href') implemented in the adehabitatHR package (Calenge, 2006). We then computed a daily NDVI value for each

group on its given home range using a linear interpolation between two known NDVI values of 16 days-intervals.

The social rank of adult females was established each year for each group separately using *ad libitum* and focal observations of dyadic agonistic interactions (supplants, displacements, threats, chases and physical attacks). We computed a linear hierarchy among adult females using Matman 1.1.4 (Noldus Information Technology, 2013), and then calculated a relative rank for each female controlling for group sizes. This relative rank was computed using the formula (N-r)/(N-1), where N was the number of adult females in the group in a given year, and r was the absolute rank of the female (ranging from 1 to N, 1 being the most dominant). Although adult females' ranks are relatively stable through time, individuals' relative ranks change as females enter and leave the hierarchy through maturation and death, respectively. Each female was assigned one relative rank per year, ranging from 0 (for the lowest ranking female) to 1 (for the highest-ranking), as hierarchy is inherited and stable for female baboons. For analyses of infant development, we considered the mother's rank during the year her infant was born.

The mother's parity was assigned using long-term life-history data. Females were considered primiparous between the birth of their first and second infant, and multiparous after the birth of their second infant.

3 Infant color scoring

Infant coloration was scored using photographs and direct field observations. An observation, which could be either from a photograph or from the field, was a set of scores of different body parts on a given day for a given infant baboon. We used photographs opportunistically taken by field observers between 2005 and 2018 of infant baboons aged between 0-19 months old (N=255 pictures of 109 infants in total, median=2 pictures per individual, range: 1-11 pictures

per individual). We discarded photographs when luminosity or quality were too poor to give a color score. In addition, in 2018 and 2019, infant baboons were scored every two weeks using direct field observations, until they finally turned completely grey. We obtained 158 field observations on 28 infants in this way, i.e. with no photograph (median=5.5 observations per individual, range: 1-10 observations per individual). Infant baboons were scored on photographs by one observer (Author 2), and in the field by one observer (Author 1). We determined the inter-individual consistency of scores by scoring independently the same set of 60 pictures, and compared score similarity with the intra-class correlation coefficient for each body part (Koo & Li, 2016). To do so, we computed intra-class coefficient looking at the absolute agreement of a single-fixed rater with a two-way mixed models, using the ICC function of the 'psych' package in R (Revelle, 2020). The scoring reliability was excellent for each body part (mean ± SD, ICC = 0.92 ± 0.06, see also Table S1 of the Supporting Information). Thus, in total, we scored coloration for 134 infants between 2005 and 2019.

In addition to determining the color of the fur covering the whole body, we scored the skin color of the following body parts: ears, eye contours, hands and feet, muzzle, muzzle tip, and ischial callosities (see Figure 1 for locations of these body parts). For each body part, we attributed a score between 1 and 5 following previous work (Altmann & Altmann, 1981; Rasmussen, 1979), such that 1 is fully pink, 2 is distinctively pinker than grey, 3 is a mixture of pink and grey, 4 is distinctively greyer than pink, and 5 is fully grey (Figure 2). For the fur, 1 is fully black, 3 is a mixture of black to grey, and 5 is fully grey; we did not use scores 2 and 4 because the color transition for the fur is less obvious than for other body parts (Figure 2). We scored all the body parts that were visible in each photograph. The data that support the findings of this study are openly available in Mendeley data: http://dx.doi.org/10.17632/65vk9tck25.1.

4 Accuracy of age estimations based on fur and skin coloration

To describe the physical transition in fur and skin coloration and further test whether it is a reliable method to estimate the age of an infant, we focused on scores from a sample of 73 infants of known age, that is, whose date of birth was known with a maximum uncertainty of 10 days. These dates of birth were determined from having been present on either the day of birth (51 infants, hereafter called Sample 1) or the day of conception (22 infants, called Sample 2). The conception day was identified as the exact day of deturgescence of the sexual swelling in the conceptive cycle, which was the cycle followed by a pregnancy and by no other cycle. We then estimated the dates of birth of these 22 infants by adding 190 days to the conception date, based on the fact that the mean gestation length is 190 days at Tsaobis with little variability (range: 181-200 days, SD = 5, N = 13 pregnancies where both conception and birth were observed). We considered only baboons aged less than 8 months, as older baboons, from 8 to 19 months old, were all fully grey. We thus restricted our dataset to this Cohort 1, comprising 242 observations from 73 infants: 148 photographs on 59 infants and 94 field observations on 16 infants (including 2 infants that were both photographed and observed in the field in 2018). Specifically, we obtained 238 scores for ears, 201 for eye contours, 238 for fur, 203 for hands and feet, 239 for muzzle, 91 for muzzle tip and 143 for ischial callosities.

To determine the body parts that showed the most reliable timing in color transition to predict ages, we computed a correlation matrix using the Spearman's rank correlation coefficient between infant age (in months) and color scores for each body part of individuals in Cohort 1. We also examined pairwise correlation coefficients between the different coloration scores to determine whether some body parts provided redundant information because they changed color at the same age. It is important to note that the dataset used to generate these correlations is pseudoreplicated to some extent given that some individuals contribute multiple observations. These correlation coefficients are nevertheless useful to compare values across

body parts, but should be interpreted with caution to evaluate the statistical significance of any single correlation.

To determine the accuracy of coloration scoring as an estimate of infants' ages, we computed the difference between the actual known age and the estimated age of another, independent subset of 70 observations on 22 infants. To do so, we divided our Cohort 1 in two sub-samples, namely Sample 1, including 172 observations of 51 infants with precisely known dates of birth (less than 10 days of uncertainty), and Sample 2, including 70 observations on 22 infants (with exactly 10 days of uncertainty on their date of birth, since it had been inferred from conception date). We use Sample 1 as the reference for age estimation at color transitions, and Sample 2 to validate our method on a fully independent sample.

With Sample 1, we first conducted a principal component analysis (PCA) taking into account the color scores of the seven body parts considered, using the function 'PCA' of the 'FactoMineR' package (Husson, Josse, Le, & Maintainer, 2020). We had a considerable number of missing values in our dataset as it was generally impossible to score all body parts from a single picture. To conduct a PCA with missing values, we performed imputations to complete the dataset using the 'imputPCA' function of the 'missMDA' package (Josse & Husson, 2016), which uses an iterative algorithm taking into account similarities between observations, as well as relationships between the scores of different body parts. The first dimension of the PCA (PC1) explained 86.6% of the variance of the color scores (versus 8.8% for the second dimension), and was the only PC retained for downstream analyses. We then investigated the relationship between PC1 and infant age (in days). To do so, we compared several linear models, all with PC1 as response variable, and containing as fixed effects a polynomial function of age modelled with variable degrees (from 1 to 8). We selected the best model of this subset as the one minimizing the Akaike Information Criterium (AIC), and a polynomial function of age of degree 4 was retained in our model.

Next, we followed four steps to quantify the accuracy of age estimation from Sample 2. First, we estimated the missing values of the Sample 2 dataset on color scores using the method described above ('missMDA' package) (Josse & Husson, 2016). Second, we predicted the values of PC1 using the color scores of the seven body parts, using the 'predict.PCA' function of the 'FactoMineR' package, that took into account the PC1 values computed from Sample 1 (Husson et al., 2020). Third, we used the linear model (that was computed on Sample 1) to calculate one age estimate for each of these predicted values of PC1, i.e. for each observation of Sample 2. More precisely, we used the 'uniroot' function in R to solve the equation of 4 degrees linking each PC1 value with infant age. Fourth, we computed the absolute difference, in days, between the actual known age (± five days of uncertainty) and this estimated age to quantify the accuracy of our method of age estimation.

In order to investigate the effect of the number of body parts that were scored on the accuracy of our age estimates, as well as which body part was the most informative in this context, we repeated this process with a variable number of body parts. From the seven body parts initially considered, we first removed the fur scores from Samples 1 and 2, as the scores of this body part had the lowest correlation with PC1. We then repeated this process by progressively removing one body part at a time, based on the relative values of the correlation between PC1 and the raw scores of that body part, removing first those parts for which scores were least correlated to PC1. Chronologically, we first removed fur, followed by hands and feet, ischial callosities, muzzle and eye contours. Our last round of analyses contained only scores from ears and muzzle tip.

We also tested whether the 5-level scale for color scores produced more accurate age estimations than a simpler 3-level scale with the following levels: (1) pink (score 1 in our 5-level scale), (2) transitional (pooling scores 2, 3, 4 in our 5-level scale), (3) grey (score 5 in our 5-level scale). Using only one score instead of three for transitional colors can facilitate data

collection in the field, and be less subjective across observers. We then repeated the same processes described for Samples 1 and 2, to quantify the accuracy of the age estimation under a 3-level scale of color scores for different number of body parts considered.

We also tested the effect of the number of observations per individual on the accuracy of age estimates. In Sample 2, there were 70 observations from 22 infants (range = 1-8, median=2 observations per infant). For all infants with more than one observation, we computed one estimated birth date by averaging the different birth date estimates from each observation. We then computed the difference, in days, between the actual and estimated birth dates as an indicator of estimation accuracy to compare the accuracy of age estimates obtained from a variable number observations of a given infant.

Moreover, we investigated the potential effects of the actual age of an infant on the accuracy of age estimations per observation, to test whether the accuracy of our age estimates may decrease for older juveniles. To do so, we ran a linear mixed model, with the accuracy of age estimates per observation (i.e. the absolute number of days between actual age and estimated age) as a response variable, the actual age as the only fixed effect, and infant identity as the only random effect (to control for repeated observations). For this analysis, we used all observations available from Sample 1, for all 7 body parts scored on a 5-level scale.

Finally, we were interested in quantifying the effects of observation types, i.e. field or photographic observations, on the accuracy of age estimation per observation. To do so, we ran a linear mixed model, with the accuracy of age estimates per observation as a response variable, the observation type as the only fixed effect, and infant identity as the only random effect (to control for repeated observations). For this analysis, we used all observations available from Sample 1, for all 7 body parts scored on a 5-level scale to estimate ages of Sample 2 (Sample 2 contained 38 field observations from 5 infants and 32 photographic observations from 17 infants).

5 Determinants of individual variation in the pace of color changes

To identify the main determinants of developmental pace, we used 242 observations from the full sample of 73 infants with known ages (Cohort 1), and ran general additive mixed models (GAMMs). We first computed a weighted mean color score for each observation, where the score of each body part was given a different weight depending on its correlation with infant age (see above). More precisely, we attributed less weight to body parts that were less correlated with age by dividing their color score by their correlation coefficient, on the basis that the developmental pace of these body parts was less variable across individuals for a given age, and so presumably less affected by environmental and individual factors. We thus obtained a general score of color development across all body parts for a given observation. Our response variable was the weighted mean color score per observation (continuous variable).

GAMMs allow to fit non-linear relationships between the response variable and one or more fixed effect(s), using thin plate splines (Wood, 2003). We first determined the best model describing the age effect on mean color scores, with the identity of infant set as random effect to take into account the lack of independence between multiple observations of a same individual. To do so, we compared GAMMs containing either (1) a simple, continuous effect of age; (2) age modelled as a polynomial of degree 2; (3) a polynomial of degree 3; or (4) age modelled using a thin plate regression spline. We selected the best model as the one minimizing the Akaike Information Criterium (AIC). We found that the age modelled using a thin plate regression spline was retained in all our models (See Table S2 in the Supporting Information for model selection on the weighted mean color score response variable for an example). We then ran our global GAMMs, with age modelled with a spline, infant identity as random effect, and including the following additional fixed effects:

- *Food availability during infant growth*. We expected infants whose gestation and birth occurred during periods of high food availability to develop faster for their age (Altmann & Alberts, 2005; Johnson, 2003). To test which time period of infant development (prenatal versus postnatal) was most sensitive to variations in food availability, we investigated the effects of both food availability during pregnancy (approximated by the mean NDVI daily values between conception and birth date for a given infant) and early lactation (approximated by the mean NDVI daily values between birth and observation date for a given infant). As these two indicators of food availability were highly correlated (Pearson correlation = 0.39, confidence interval: [0.28; 0.49], t=6.58, P-value<10^{-4}), leading to collinearity, we included them separately in two different models.

- *Date of birth*. We expected infants born at particular times of the year to develop more quickly. The NDVI is only a partial proxy of food availability, and other components of seasonal variation that are not necessarily captured by NDVI (such as temperature, photoperiod, or particular plant phenologies) may further affect developmental pace. As a given date in the annual cycle is a circular variable (at least when considering environmental seasonality), we used a sine fixed effect expressed as follows to introduce the infant's date of birth, converted in radians, into our multivariate linear model:

$$\sin\left(Infant's\ date\ of\ birth + \varphi\right)$$

Where φ is the phase value. We changed the phase value φ (to 0, π/6, π/3, π/2, 2*π/3, 5*π/6) to account for potential phase shifts across the year, i.e. to consider all the months of the year as possible birth months maximizing faster development. For example, a positive effect of the sine phase of π/6 would maximize February, and a negative effect will maximize August. We ran sequentially six different multivariate models (GAMMs with the six different phase values) containing all other fixed effects, and we selected the best phase as the one minimizing the AIC (which is π/3 for the weighted mean color score model).

- *Mother's dominance rank*. We expected infants from dominant females to develop more quickly, following studies on other aspects of baboon developmental pace (Altmann & Alberts, 2005; Cheney et al., 2004; S. Johnson, 2003).

- *Mother's parity*. We expected infants from primiparous mothers to develop more slowly, following studies on other aspects of baboon developmental pace (Altmann & Alberts, 2005).

- *Infant sex*. We did not expect any sex difference in the pace of early morphological development, following studies on other aspects of baboon developmental pace (Altmann & Alberts, 2005; Altmann & Altmann, 1981; Johnson & Kapsalis, 1995). Nevertheless, we included this variable to control for potential unexpected sex differences.

- *Group identity*, to control for possible differences between social groups.

We further considered each body part separately (seven models) to test whether the same determinants affected all body parts or only some of them, and to evaluate which body parts were most sensitive to ecological, individual and maternal traits. Here, our response variables were the scores of one given body part, and were coded as ordinal, with five categories for each body part (except for the fur, with only three categories). We ran all the GAMMs using the 'gam' function of the 'mgcv' package (Wood, 2003), in R version 3.5.0 (R Core Team, 2018). Ordinal response variables for each body part were specified with the family 'ocat' of the 'mgcv' package (Wood, 2003). We computed parameter estimates for each fixed effect, with Wald statistic tests (X_2) and P-values associated. For smooth effects, we computed the effective degrees of freedom, with the Wald statistic test and the P-value. We considered an effect to be significant when its P-value was < 0.05. We were also interested in quantifying the importance of inter-individual variation in developmental pace, and so tested the significance of the random intercept, looking similarly at its P-value. For each model, we also checked graphically the normality of the residuals' distribution and the accuracy of the number of knots used for the

age thin plate spine (this parameter constrains the 'wiggliness' of the smooth, i.e. the number of bow points in the fitted curve) (Wood, 2003) using the 'gam.check' function of the 'mgcv' package (Wood, 2019). Graphical representations were made using the 'mgcViz' package (Fasiolo, Nedellec, Goude, & Wood, 2018).

RESULTS

1 Characterization of fur and skin color changes in chacma baboon infants

All results associated with the characterization of fur and skin color changes in relation to age are summarized in Figure 3. All baboons were fully grey (i.e., at all body parts) after 8 months of age, with similar fur and skin coloration as adults. The fur, muzzle or hands and feet were the first body parts to turn grey, on average between 1 and 2 months of age. Hands and feet, as well as the muzzle, started to transition around 1 month old until becoming fully grey at approx. 4 months of age. Ears started to turn grey after 2 months and were totally grey by 5 months. The last body parts to change color were the eye contours, the ischial callosities, and the tip of the muzzle, which started to transition at approx. 3 months of age, and finished after 5 months. The qualitative chronology of the transition was apparent in the correlation matrix (Table 1): hands and feet scores were highly correlated with muzzle scores, and eye contours scores were highly correlated with muzzle tip scores. Nonetheless, the order in which body parts change color was not always consistent across individuals. For some infants, we observed ears turning grey before muzzles and hands, or ischial callosities turning grey before the muzzle tip and ears. Overall, a chacma baboon infant with entirely pink skin and black fur was almost always younger than 2 months old, as at least the hands and feet started to turn grey after this age. An infant with entirely grey skin and fur was at least 4 months old, as no infant was observed with a grey tip of the muzzle before this age. Finally, a transitional infant was aged between 1 and 6 months old.

2 Accuracy of age estimates based on color scores

The color scores were strongly correlated with the known ages of infants for all body parts, though correlation coefficients were slightly lower for the fur and the ischial callosities (Table 1). This means that the scores of these two body parts produce less precise age estimates, probably due to higher inter-individual variation in the age of transition of these parts compared to others. For example, a 3-month-old baboon could exhibit the full range of colors for ischial callosities, from fully pink to fully grey; and a 1-month-old baboon could exhibit a fully black or a fully grey fur (Figure 3).

In order to test the accuracy of infant body coloration as a method of age estimation, we computed a composite score (using PCA) from 172 observations of all body parts from 51 infants of known ages (births observed, Sample 1), and then predicted this composite score to estimate ages on an independent sample of 70 observations from 22 infants of known ages (Sample 2). We obtained a median difference of 12 days between the actual age and the estimated age using 70 observations, 7 body parts and a 5-level scale of color scores (Table 2). We also investigated the effects of the number of body parts considered, and the number of levels of the color scale. Decreasing the number of body parts considered only slightly decreased the accuracy of age estimates (Table 2), and the same conclusion applied for using a 3-level color scale instead of a 5-level one – though using a 3-level scale in combination with few body parts decreased accuracy more substantially (Table 2). Our best age estimations per observation were computed when considering the skin across all 6 body parts but excluding the fur, and using a 5-level color scale (absolute number of days of between actual and estimated ages: median = 10.7, range = 0.1–86.4). We also investigated the effect of the number of observations per infant on the accuracy of age estimates: the more observations, the more accurate were the estimates (Figure S1, Supporting Information). Finally, the accuracy of age

estimates significantly decreased with age (X_2 = 10.0, P-value = 1.54x10^{-3}) (Figure S2, Supporting Information), and were lower for photographic compared to field observations (Figure S3, Supporting information), albeit the latter effect did not reach significance (X_2 = 3.63, P-value =0.06).

3 Determinants of individual variations in the pace of color changes

Finally, we investigated the determinants of inter-individual variations in age-related color scores, looking at ecological (food availability during pregnancy or during early-lactation, birth timing), maternal (parity, rank) and individual (sex) predictors using GAMMs controlling for age with a spline regression (Figure 4). The model explained 93% of the variation in the weighted mean color scores. We detected significant inter-individual differences in mean color scores (Table 3), and in most body parts (except for the muzzle tips, for which we had fewer infants scored compared to other parts, see Table S3 in Supporting Information). Our index of food availability during pregnancy influenced the weighted mean color score (controlled for age): infants turned grey earlier considering all their body parts together when food during pregnancy was abundant (Table 3, Figure 5). In contrast food availability during lactation did not (Table S4, Supporting Information). We did not detect any effect of maternal (rank and parity) nor individual (birth date and sex) traits on variation in infant mean color scores controlled for age (Table 3). Looking at individual variation in color transitions for each body part separately, we found a positive effect of food availability during pregnancy on the score of ischial callosities only (Table S3, Supporting Information). We also found a positive effect of the timing of birth on the scores of muzzle tips (maximizing scores for infants born in December-January) but not for other body parts (Table S3, Supporting Information). We did not detect any effect of food availability during lactation, maternal traits, i.e. maternal rank and parity, on variation in infant color for any body part (Table S3, Supporting Information).

DISCUSSION

Our purpose in this study was twofold: (1) to assess how well infant chacma baboons with unknown ages can be aged on the basis of their skin and fur color, and (2) to explore potential environmental, maternal, and individual predictors of variation in the pace of infant color development for infants with known ages. The age estimates obtained using infant color scores were generally accurate (median number of days between actual age and estimate age per observations = 10, range=0-86 days). All the tools required for estimating ages in a chacma baboon population are provided in this paper. Figures 1 and 2 can be used to score baboon coloration directly in the field (or using photographs), and the methods section details how the first dimension of a composite score (using PCA), derived from these color scores, can be computed to estimate ages. Various recommendations can be made to improve the accuracy of age estimates:

1. Use the color scores from all body parts except fur, as age estimates were most accurate with this configuration. However, decreasing the number of body parts considered does not decrease the accuracy of age estimations dramatically. For example, considering only two body parts (ears and muzzle tip) instead of six reduces the accuracy of age estimations by only 4.5 days. Nonetheless, such a result may vary across primate species, and one should establish the relevant body parts to be considered in different species.
2. Score the same individual repeatedly, as an infant with 8 observations had a birth date estimation error of 5 days in average, compared to more than 30 days for infants with only a single observation. Ideally, infants should be scored as early as possible (as accuracy decreases as infants age) and regularly until it turns fully grey.

3. Prioritize field observations. Photographic evidence can be less accurate because color scores may be influenced by fluctuating light conditions. If necessary, photographic approaches should exploit multiple high-resolution photographs of the same individual on a given day at different times and angles to control for light variation.
4. Consider using a 3-level color scale, which is slightly less accurate than a 5-level scale but also more practical, and may maximize inter-observer reliability. However, such choice depends on the trade-off between the accuracy targeted and the conditions of data collection (e.g., single versus multiple observers).

In addition, this study opens the possibility of a similar application for machine learning where an algorithm could predict the age of an infant based on pictures, as long as a large set of high-quality pictures (see recommendation #3) of known-age individuals is available to initialize the algorithm. This relatively recent method is based on mathematical and statistical approaches through which computers can 'learn' from data to then make predictions. Such methods have been used in a wide range of field applications, and are becoming increasingly common (Al-Jarrah, Yoo, Muhaidat, Karagiannidis, & Taha, 2015).

Changes in the pigmentation of infants' ears and muzzles at Tsaobis follow a similar pattern to that observed in another population of wild chacma baboon living in Mkuzi Game Reserve (South Africa), with an onset of grey coloration appearing around 1-2 months, and the full transition completed around 4-6 months of age (Whitehead et al., 1990). Our detailed characterization of the age at which fur and skin turn grey indicates that infant chacma baboons' coloration develops faster than yellow baboons (Altmann & Altmann, 1981; Rasmussen, 1979). Whilst chacma baboon infants have all turned grey by 8 months of age, most yellow baboon infants are still in the transition phase at this age, and only exhibit adult color around 12 to 14 months of age, depending on the population (Altmann & Altmann, 1981; Rasmussen, 1979). In addition, in contrast to yellow baboons, the order in which body parts change color was not

524 always consistent across individuals in this study. Discrepancies observed in the age and
525 chronology of transition between baboon species highlight that such patterns are species-
526 specific, and that the methodology presented here should be developed and validated separately
527 for each species.

528 Inter-individual variation in the rate of maturation was high for each body part considered
529 in this study, as found in yellow baboons (Altmann & Altmann, 1981; Rasmussen, 1979).
530 Specifically, the change in fur color was a less accurate indicator of age, as fur turned grey
531 relatively early and showed marked individual variation. Failure to derive accurate age
532 estimates remains non-negligible (we had a maximum of 86 days difference between actual and
533 estimated age when relying on 6 body parts), due to the existence of outlier individuals with
534 very fast or slow development. This suggests that, whilst this method of age estimation is not
535 perfect, infant coloration can provide a simple and non-invasive proxy to detect individual
536 variation in developmental pace on a semi-quantitative scale. Nevertheless, despite their utility
537 for tracking other developmental factors (Barthold et al., 2009; Treves, 1997), studies linking
538 age-related changes in color to other indicators of developmental pace are very rare in baboons.
539 Only one study on Amboseli yellow baboons recorded that late changes in paracallosal skin
540 color can be seen as a first sign of developmental abnormality, being followed by delayed
541 maturation, locomotor disability and finally death (Altmann & Altmann, 1981).

542 Regarding the determinants of individual variations in color-for-age considering all body
543 parts together, we found that higher food availability during pregnancy, but not during early-
544 lactation, accelerated the transition towards adult coloration. In line with this, infant yellow
545 baboons from a food-enhanced group grew more rapidly than individuals from wild-foraging
546 groups (Altmann & Alberts, 2005). Similarly, in Phayre's leaf monkeys (*Trachypithecus*
547 *phayrea*) infants in larger groups transitioned from natal to adult fur color later, suggesting that
548 food competition affects infant color maturation and development (Borries et al., 2008). Here,

549 we distinguished pre-natal from post-natal food availability, and our results emphasize the
550 importance of maternal condition during pregnancy for infant post-natal color development. In
551 capital breeders like baboons or humans, females can store energy to use it later, and conception
552 likelihood generally peaks during periods of high food availability to increase the success of
553 their reproductive attempt (Brockman & van Schaik, 2005). Numerous human studies similarly
554 show that maternal nutritional status during pregnancy has a significant impact on infant birth
555 weight, early-life development, health and survival (Emery Thompson, 2013; Martorell &
556 Gonzalez-Cossio, 1987). This study, by highlighting the effect of prenatal food availability on
557 inter-individual variations in color-for-age, suggests that similar effects could occur in baboons,
558 and that color-for-age may thus be a reliable indicator of other developmental dimensions.
559 Studies on various primates including baboons have also shown that the infants of dominant
560 females exhibit faster development in terms of growth rate and age at weaning (Altmann &
561 Alberts, 2005; Fedigan, 1983; Pusey, 2012). Yet, surprisingly, maternal rank did not affect
562 individual variation in infant color in this study. Given that color scores reflect inter-individual
563 variation in maternal nutritional condition (see above), it is possible that rank does not capture
564 such differences at Tsaobis, perhaps because most food resources are not monopolizable, or
565 because subordinate females adopt foraging and social strategies that help to mitigate the costs
566 of their low rank (Marshall, Carter, Ashford, Rowcliffe, & Cowlishaw, 2015; Sick et al., 2014).
567 Interestingly, looking at the color development of each body part separately, we found that
568 the only body part affected by prenatal food availability was the ischial callosities. This suggests
569 that the color scoring of different body parts could be used for different purposes; for example,
570 ischial callosities are a better indicator of developmental pace than of age. Further investigations
571 of the determinants of color changes at specific body parts showed that infants born in
572 December-January have greyer muzzle tips for their age than others. However, the muzzle tip
573 was scored on the lowest number of infants (N = 16), and such a small sample size questions

574 the robustness of this result that was not replicated using other body parts. Using a larger dataset
575 will be necessary to reach conclusive results.

576 Our study of the determinants of inter-individual variation of color-for-age is preliminary
577 for several reasons. First, we were not able to explore the impact of other factors that are known
578 to influence infant color transitions, like variation in social dynamics and infanticide risk
579 (Bădescu et al., 2016) that are probably of considerable evolutionary significance for young
580 chacma baboons (Cheney et al., 2004; Palombit, 2003). Second, further studies are needed to
581 explore the correlation between age-related changes in coloration and developmental
582 milestones like weaning age for chacma baboons. Testing whether color development co-varies
583 with other dimensions of development would indicate if it could be used as a reliable indicator
584 of developmental pace that may ultimately be connected to fitness. In line with this suggestion,
585 the transition from natal to adult fur coloration of wild ursine colobus (*Colobus vellerosus*)
586 infants has been used as a proxy of developmental pace to show that high infanticide risk
587 accelerates infant development (Bădescu et al., 2016). Finally, examining the potential effects
588 of infant coloration on protective behavior from other group members, and on the level of
589 alloparenting care received wherever it is relevant (Brent, Teichroeb, & Sicotte, 2008; Ross &
590 Regan, 2000) could be an interesting perspective to test other hypotheses proposed to account
591 for the evolution of natal coat in primates.

592 Our study demonstrates that monitoring the skin color transition of infant baboons is a non-
593 invasive and accurate method to estimate age up to 8 months old, with a median accuracy of 10
594 days, which can decrease further if the same individual is scored repeatedly. Our study
595 additionally highlights inter-individual variability in the ages of color transitions. This suggests
596 that scoring the change in infants' body coloration can also be used to detect individual variation
597 of developmental pace, and certain body parts are more variable than others for a given age,
598 and thus represent promising candidates in this respect. In this context, food availability during

prenatal life affected infant color-for-age in our population, suggesting that maternal nutritional condition during pregnancy plays a central role in infant color development. Further research is necessary to determine whether such scores correlate with broader aspects of development (morphological, behavioral, and physiological), and which body parts are most useful.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Mendeley data: http://dx.doi.org/10.17632/65vk9tck25.1

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CONFLICT OF INTEREST STATEMENT

The authors do not have any conflict of interest to declare.

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FIGURE LEGENDS

Figure 1: Picture of an infant chacma baboon showing the different body parts scored in this study.

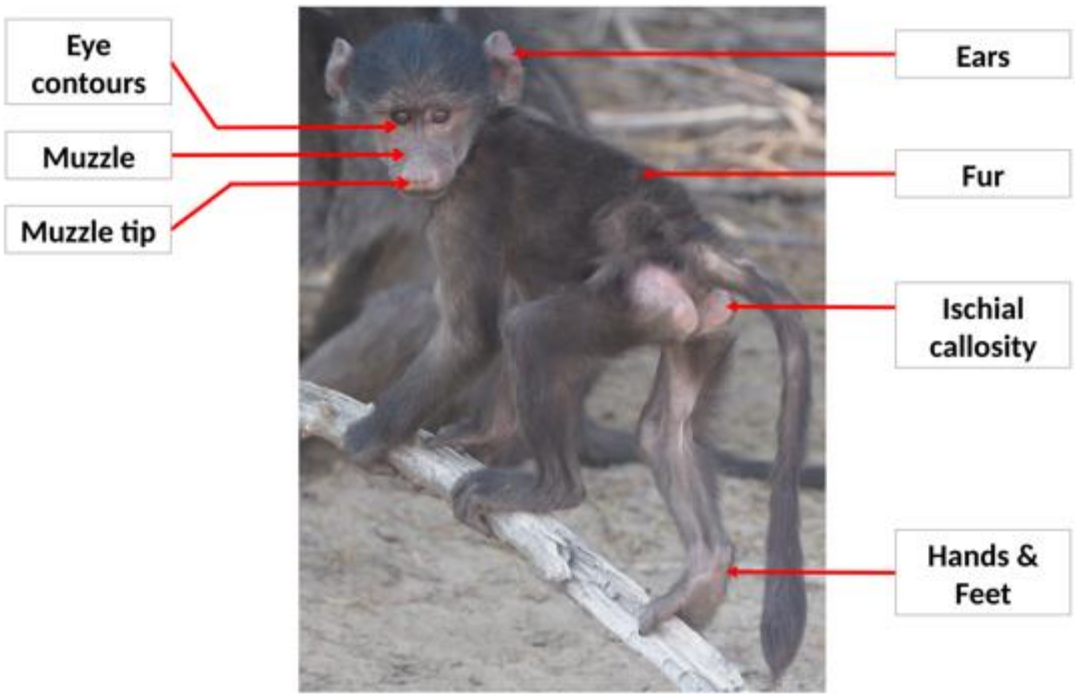


Figure 2: Pictures showing examples of color scores for different body parts. The first column refers to score 1, i.e. pink skin for each body part, and black fur. The second column refers to score 2, i.e., body parts that are pinker than grey (this score did not exist for fur). The third column refers to score 3, i.e., body parts that are just as pink as grey (and for fur, just as black as grey). The fourth column refers to score 4, i.e., body parts that are greyer than pink (this score did not exist for fur). The last column refers to the score 5, i.e. grey for all body parts as well as for fur.

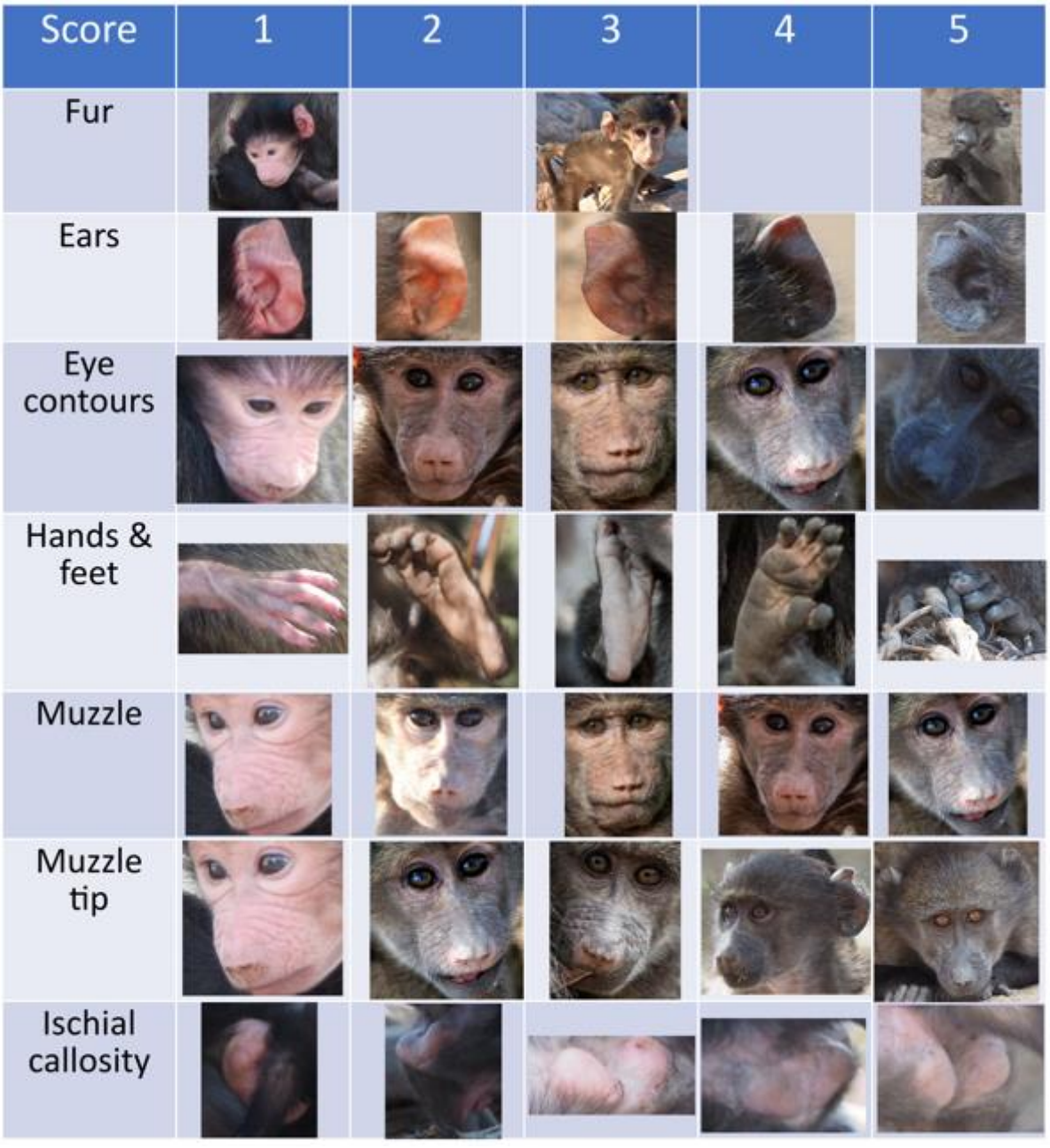


Figure 3: Color scores (from 1 to 5) of the different body parts of an infant according to its age (in months), using 242 observations on 73 infants with known birth date (Cohort 1). Month 0 indicates an infant less than 1 month old, Month 1 indicates an infant aged between 1 and 2 months old, etc. Each boxplot color represents a body part (see legend for details, ISC refers to ischial callosities). The median value for each boxplot is represented by a diamond, and outlier points are indicated by dark red dots.

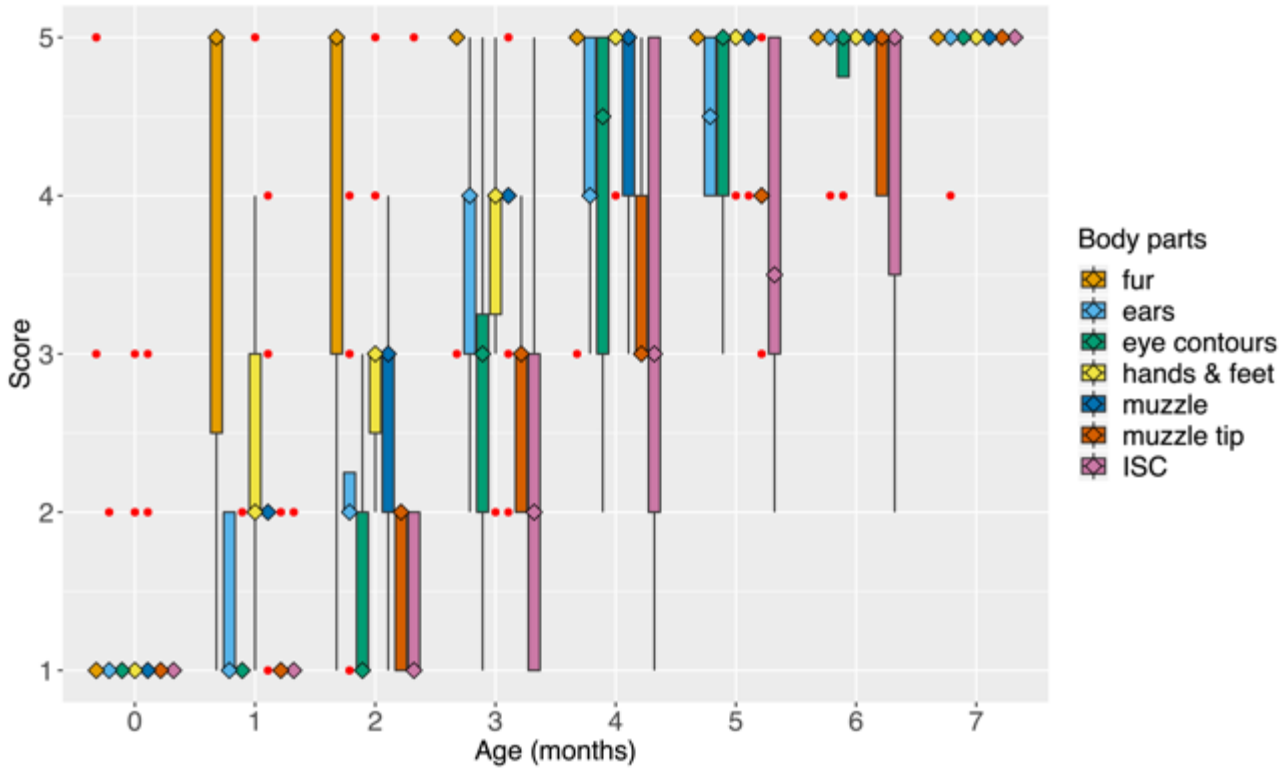


Figure 4: Weighted mean color score according to infant age (in days). Each dot represents the age component smooth function of the weighted mean color score according to individual age. The red curve shows the fitted smooth effect, and the 95% upper and lower confidence intervals are represented by the dashed blue curves.

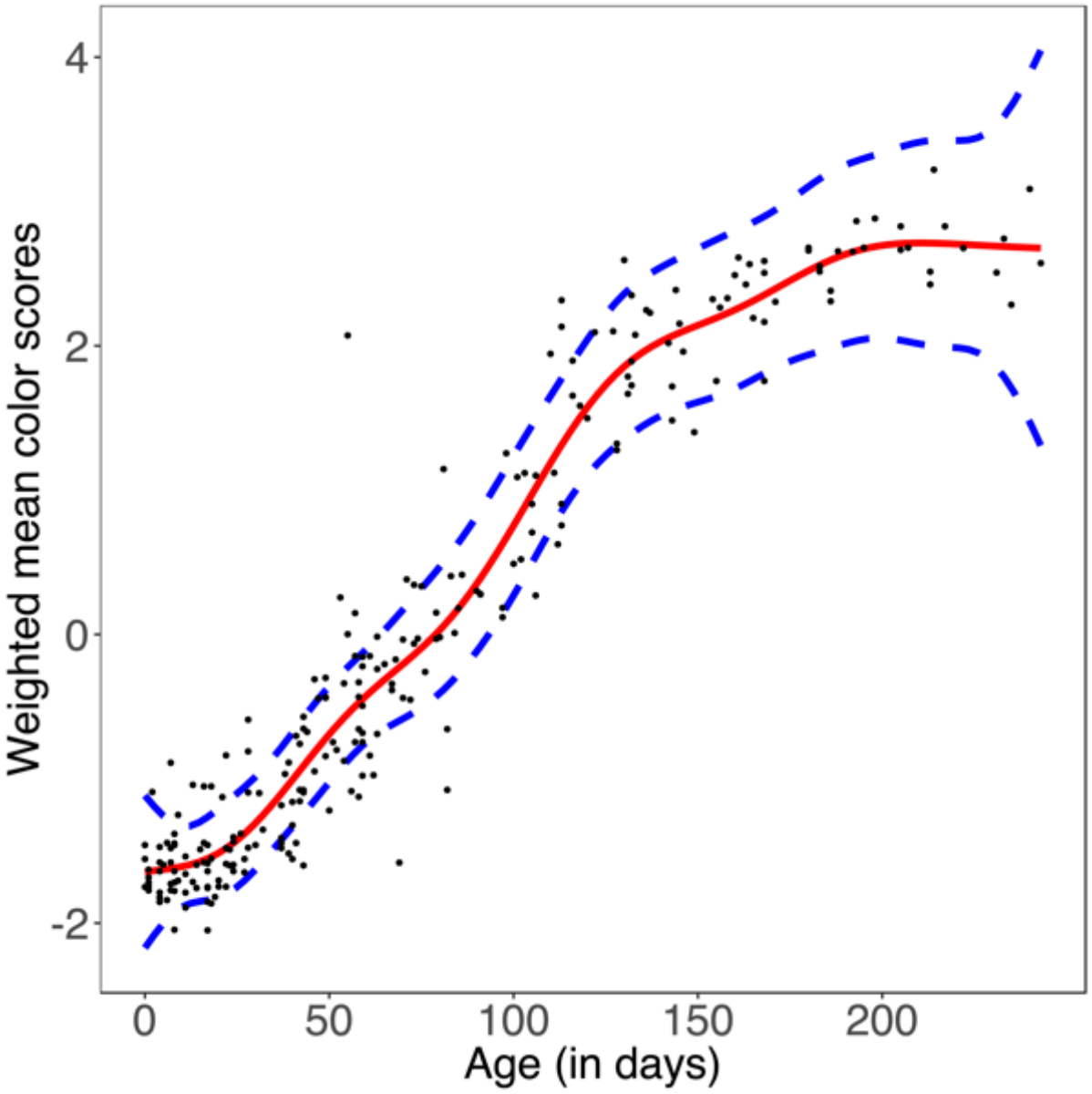
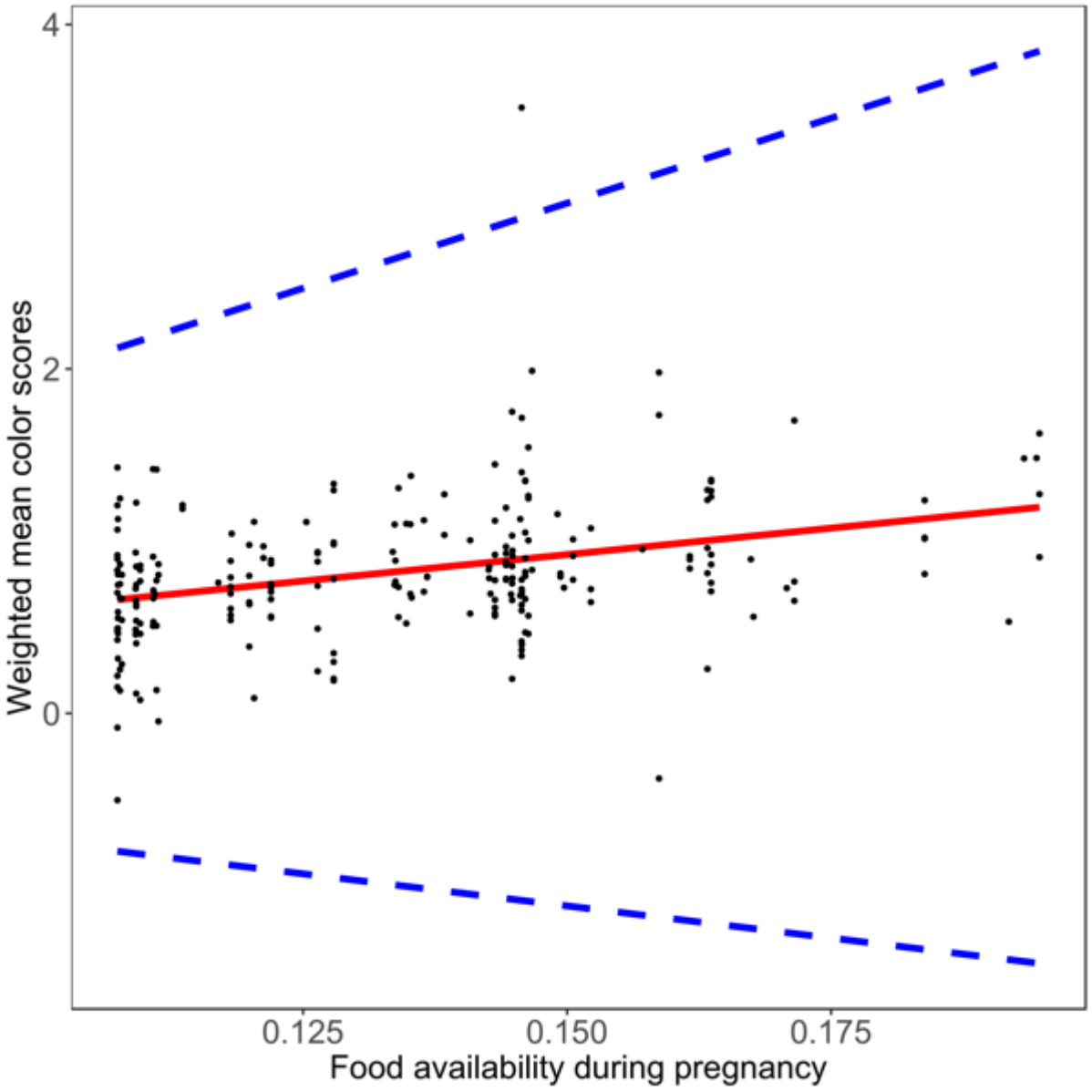


Figure 5: Effect of food availability during pregnancy on infant weighted mean color scores, controlled for infant age, identity and all other fixed effects included in our GAMM. Each dot represents an observation (raw values). The red curve shows the fitted linear effect of food availability, and the dashed blue curves represent the 95% upper and lower confidence intervals.



Tables for:

Developmental transitions in body color in chacma baboon infants: implications to estimate age and developmental pace

TABLE 1: Correlation table between known ages and age estimates for each body part. The correlation matrix was built using Spearman rank coefficients and using the full sample (242 observations from 73 infants).

Variable	Age (Months)	Fur	Ears	Eye contours	Hands & feet	Muzzle	Muzzle tip
Fur	0.86						
Ears	0.93	0.86					
Eye contours	0.90	0.84	0.92				
Hands & feet	0.95	0.89	0.94	0.92			
Muzzle	0.93	0.88	0.94	0.92	0.97		
Muzzle tip	0.91	0.85	0.93	0.95	0.92	0.93	
Ischial callosity	0.81	0.78	0.82	0.88	0.82	0.82	0.87

TABLE 2: Accuracy of age estimates using 70 observations from 22 infants (Sample 2), depending on the number of body parts considered, and on the number of levels of the color-scoring scale (3 or 5). Accuracies were measured by the absolute number of days between actual and estimate age for each observation, which are given with their median and range.

Number of body parts considered †	7	6	5	4	3	2
5-level color scale						
Median	12.2	10.7	12.9	10.9	16.4	15.2
Range	0.1 - 95.3	0.1 - 86.4	0.1 - 79.2	0.5 - 87.3	0.5 - 82.4	1.4 - 70.8
3-level color scale						
Median	11.5	11.9	12.8	15.5	17.0	18.5
Range	0.1 - 93.2	0.2 - 95.0	0.1 - 97.0	0.6 - 70.9	1.2 - 74.5	0.1 - 70.2

†: We considered respectively the scores of the ears, muzzle tips, eye contours, muzzles, ischial callosities and hands and feet when 6; of the ears, muzzle tips, eye contours, muzzles and ischial callosities when 5; ears, muzzle tips, eye contours and muzzles when 4; ears, muzzle tips and eye contours when 3; and finally ears and muzzle tips when 2.

838 **TABLE 3**: Determinants of inter-individual variation in weighted mean color scores. We
839 computed parameter estimates (with their standard deviations) for each fixed effect, the Wald
840 statistic (X_2) test, and P-values. For categorical parameters, the tested category is indicated
841 between brackets. Food availability was indexed by the mean daily NDVI during pregnancy
842 and an infant's birth timing in the annual cycle was represented by a sinusoidal term (with a
843 phase of π /3). For smooth effects, we gave the effective degrees of freedom (Edf), the residual
844 degree of freedom (Ref.df), the Wald Statistic (X^2) and the P-value. Significant effects are
845 indicated in bold. Similar models were run on each body part separately, and corresponding
846 results are presented in the electronic supplementary materials (Table S3).

Fixed effects	Estimate	Standard error	X^2	P-value
Intercept	**2.88**	**0.11**		
Food availability during pregnancy	**0.13**	**0.06**	**5.10**	**0.025**
Birth timing	0.06	0.10	0.33	0.57
Sex (Male)	0.03	0.12	0.08	0.77
Rank	0.10	0.06	2.63	0.11
Parity (Primiparous)	0.10	0.18	0.31	0.58
Group (L)	0.15	0.12	1.60	0.21
Smooth effects	Edf	Ref.df	X^2	P-value
Age	**7.10**	**8.03**	**219.9**	**$<1.10^{-3}$**
Infant identity	**40.9**	**66**	**1.88**	**$<1.10^{-3}$**

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Supporting Information for:

Developmental transitions in body color in chacma baboon infants: implications to estimate age and developmental pace

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Table S1: Intra-class coefficients (ICC) for each body part. We also computed the 95% confidence limits for ICC of each body part (ICC lower and upper limits), and indicated the number of observations used for this test (N), which varies across body parts.

Body Part	ICC	ICC lower	ICC upper	N
Fur	0.8	0.71	0.86	60
Ears	0.96	0.93	0.97	58
Eye contours	0.96	0.93	0.97	55
Hands & Feet	0.93	0.89	0.96	38
Muzzle	0.94	0.90	0.96	58
Muzzle tip	0.96	0.93	0.97	54
Ischial callosity	0.9	0.66	0.97	8

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878 **Table S2:** Model selection performed to identify the best age fit to predict weighted mean
879 color scores. We ran four GAMMs with infant identity set as random effect and different
880 functions of age as fixed effects. For each model, we computed the log likelihood, degrees of
881 freedom, Akaike Information Criterion (AIC) and ΔAIC which is the AIC value between a
882 given model and the model with the lowest AIC (indicated in bold).

Age effect	Log Likelihood	Model degrees of freedom	AIC	ΔAIC
Age	-140.9	52.9	387.7	53.6
Age + Age^2	-141.7	46.5	376.5	42.4
Age + Age^2 + Age^3	-118.2	51.6	339.5	5.4
spline(Age)	**-112.91**	**54.1**	**334.1**	**0**

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884 **Table S3**: No significant effects of food availability during early-lactation on variation in
885 weighted mean color scores. We computed parameter estimates (with their standard
886 deviations) for each fixed effect, Wald statistics (X^2) and P-values. For categorical
887 parameters, the tested category is indicated between brackets. For smooth effects, we gave the
888 effective degrees of freedom (Edf), the residual degree of freedom (Ref.df), the Wald Statistic
889 (X^2) and the P-value. The food availability was indexed by the mean daily NDVI between
890 infant birth and observation date (i.e. during lactation), and an infant's birth timing in the
891 annual cycle was represented by a sinusoidal term of its date of birth, with a phase of $\pi/3$.
892 Significant effects are indicated in bold.

Fixed effects	Estimate	Standard error	X^2	P-value
Intercept	**2.89**	**0.11**		
Food availability during lactation	0.07	0.05	1.91	0.17
Birth timing	-0.05	0.10	0.22	0.64
Sex (Male)	0.03	0.12	0.08	0.78
Rank	0.10	0.06	2.54	0.11
Parity (Primiparous)	0.12	0.19	0.43	0.78
Group (L)	0.12	0.12	1.02	0.31
Smooth effects	Edf	Ref.df	X^2	P-value
Age	**7.10**	**8.04**	**221.2**	**$<1.10^{-3}$**
Infant identity	**41.5**	**67**	**2.04**	**$<1.10^{-3}$**

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Table S4: Determinants of variation in color scores for each body part. We computed parameter estimates (with their standard deviations) for each fixed effect, Wald statistics (X^2) and P-values. For categorical parameters, the tested category is indicated between brackets. For smooth effects, we gave the effective degrees of freedom (Edf), the residual degree of freedom (Ref.df), the Wald Statistic (X^2) and the P-value. We indicated the number of observations (Nobs) and of scored individuals (Nind) for each response variable, i.e. for each body part. The food availability was indexed by the mean daily NDVI between infant conception and birth (i.e. during pregnancy), and an infant's birth timing in the annual cycle was represented by a sinusoidal term of its date of birth (with a phase of 0 for fur, $\pi/6$ for eye contours, $\pi/3$ for hands and feet and muzzle, and $\pi/2$ for ears, muzzle tips and ischial callosities). Significant effects are indicated in bold. Note that given the number of models (n=7), the significance threshold falls to α=0.007 when applying a Bonferroni correction.

Scores of body part (response variable)	Fixed effects	Estimate	Standard error	X^2	P-value
Fur (Nobs=239 on Nind=73)	Intercept	-3.68	3.96		
	Food availability	40.1	26.8	2.25	0.13
	Infant date of birth	0.57	0.81	0.49	0.48
	Group (L)	-0.07	1.10	0.01	0.95
	Sex (Male)	-0.09	1.07	0.01	0.93
	Rank	0.58	1.68	0.12	0.73
	Parity (Primiparous)	-0.72	1.73	0.17	0.68
	Smooth effects	EDF	Ref.df	X^2	P-value
	Age	**3.75**	**4.58**	**73.8**	**$<1.10^{-3}$**
	Infant identity	**32.8**	**66.0**	**75.4**	**$<1.10^{-3}$**
Ears (Nobs=238 on Nind=73)	Intercept	-0.55	2.54		
	Food availability	9.35	16.67	0.31	0.58
	Infant date of birth	1.10	0.66	2.79	0.09
	Group (L)	1.19	0.71	2.84	0.09
	Sex (Male)	-0.19	0.71	0.07	0.79
	Rank	1.06	1.09	0.94	0.33
	Parity (Primiparous)	-0.15	1.13	0.02	0.89
	Smooth effects	EDF	Ref.df	X^2	P-value

	Age	**2.94**	**3.65**	**455.4**	**<1.10-3**
	Infant identity	**21.96**	**66.0**	**49.9**	**<1.10-3**
Eye contours (Nobs=202 on Nind=64)	Intercept	-11.4	5.11		
	Food availability	59.3	30.3	3.83	0.05
	Infant date of birth	1.02	1.25	0.66	0.42
	Group (L)	1.28	1.51	0.72	0.40
	Sex (Male)	3.19	1.56	4.21	0.04
	Rank	1.91	2.33	0.68	0.41
	Parity (Primiparous)	-1.39	2.24	0.38	0.54
	Smooth effects	EDF	Ref.df	X^2	P-value
	Age	**3.24**	**4.00**	**260**	**<1.10-3**
	Infant identity	**24.0**	**57.0**	**96.7**	**<1.10-3**
Hands & feet (Nobs=204 on Nind=66)	Intercept	4.14	3.24		
	Food availability	6.97	21.8	0.10	0.75
	Infant date of birth	0.89	0.90	0.96	0.33
	Group (L)	0.49	1.00	0.24	0.62
	Sex (Male)	-0.49	1.01	0.24	0.63
	Rank	1.67	1.60	1.08	0.30
	Parity (Primiparous)	-1.21	1.53	0.63	0.43
	Smooth effects	EDF	Ref.df	X^2	P-value
	Age	**3.33**	**4.11**	**325**	**<1.10-3**
	Infant identity	**33.9**	**59.0**	**120**	**<1.10-3**
Muzzle (Nobs=240 on Nind=73)	Intercept	-1.88	3.84		
	Food availability	46.7	24.8	3.55	0.06
	Infant date of birth	1.81	1.00	3.24	0.07
	Group (L)	0.98	1.09	0.81	0.37
	Sex (Male)	2.25	1.11	4.07	0.04
	Rank	1.57	1.70	0.86	0.35
	Parity (Primiparous)	-0.40	1.62	0.06	0.81
	Smooth effects	EDF	Ref.df	X^2	P-value
	Age	**3.83**	**4.67**	**451**	**<1.10-3**
	Infant identity	**42.7**	**66.0**	**184**	**<1.10-3**
Muzzle tip (Nobs=92 on Nind=16)	Intercept	3.74	9.47		
	Food availability	-26.0	79.4	0.11	0.74
	Infant date of birth	**3.59**	**1.16**	**9.65**	**2.10-3**
	Group (L)	0.50	0.98	0.26	0.61
	Sex (Male)	-0.31	1.01	0.09	0.76
	Rank	1.46	1.53	0.91	0.34
	Parity (Primiparous)	-0.69	2.30	0.09	0.76
	Smooth effects	EDF	Ref.df	X^2	P-value
	Age	**1.00**	**1.00**	**138**	**<1.10-3**
	Infant identity	0.76	9.00	0.89	0.31

Ischial callosity (Nobs=144 on Nind=47)	Intercept	-9.66	3.24		
	Food availability	**65.1**	**20.2**	**10.4**	**1.10^{-3}**
	Infant date of birth	2.06	0.83	6.18	0.01
	Group (L)	-0.59	1.00	0.35	0.00
	Sex (Male)	0.00	1.02	0.00	0.99
	Rank	1.44	1.68	0.73	0.39
	Parity (Primiparous)	1.60	1.52	1.12	0.29
	Smooth effects	EDF	Ref.df	X^2	P-value
	Age	**1.00**	**1.00**	**98.8**	**$<1.10^{-3}$**
	Infant identity	**17.9**	**40.0**	**42.0**	**$<1.10^{-3}$**

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Figure S1: Decreased inaccuracy of infant estimated birth dates (in days) in relation to the number of observations per infant. The inaccuracy is the absolute number of days between an infant actual birth date and its estimated birth date. The red curve shows the linear fit, and the shaded area indicates the 95% confidence interval around it.

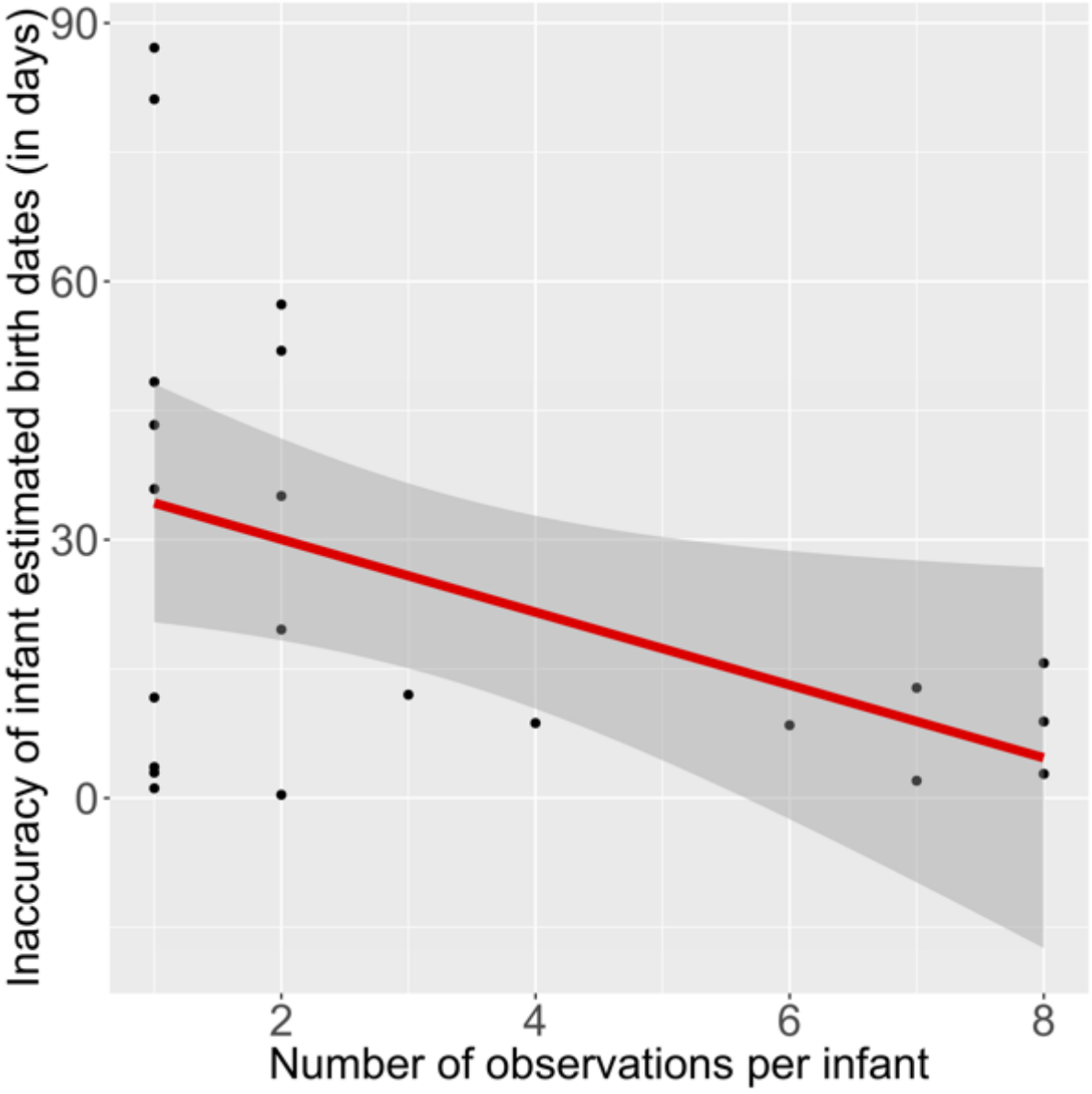

Figure S2: Increased inacurracy of age estimation (in days)in relation to the actual age of the infant (in days). The inaccuracy is the absolute number of days between an infant actual and estimated age per observation. The red curve shows the linear fit, and the shaded area indicates the 95% confidence interval around it.

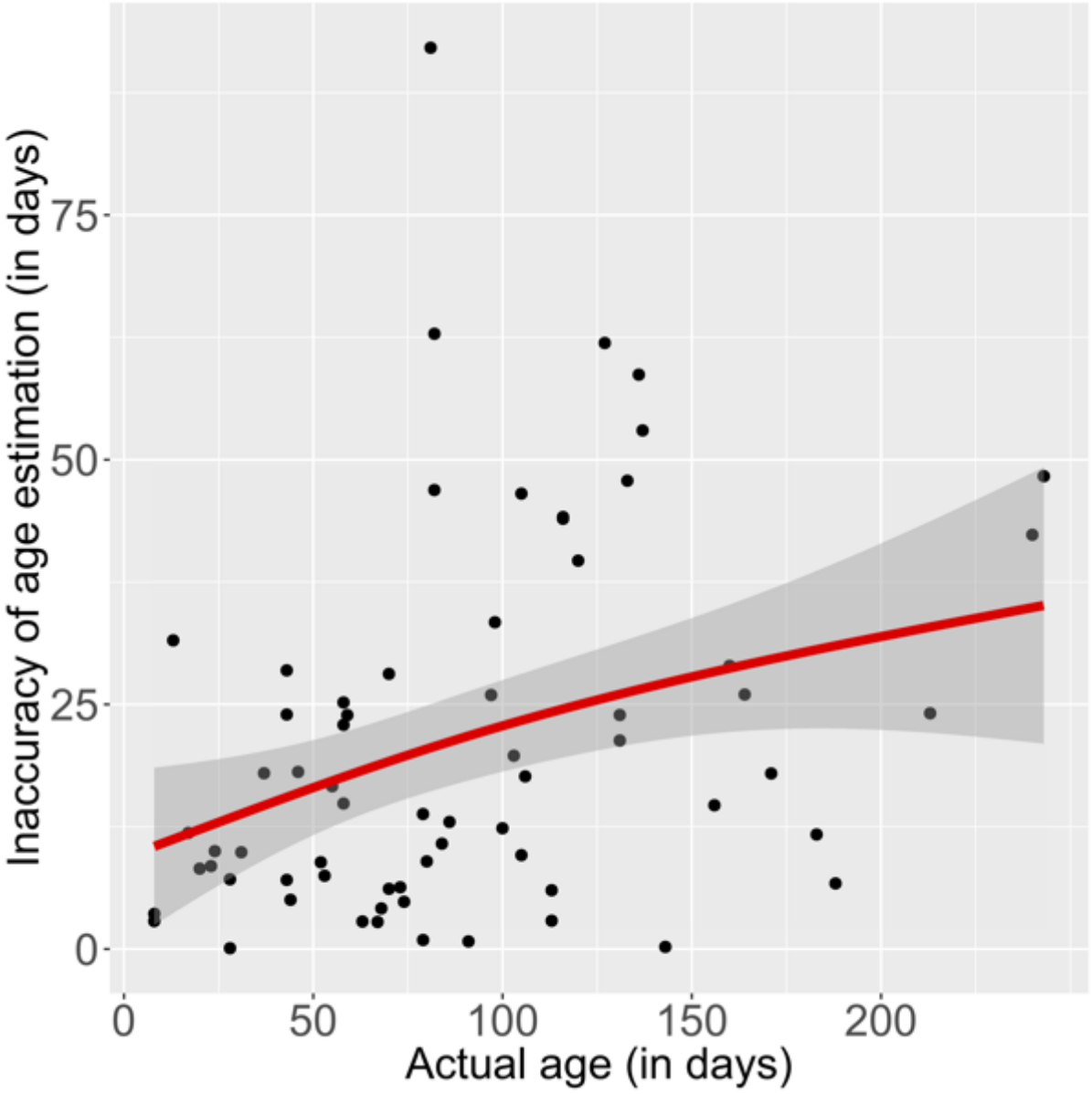

Figure S3: Inaccuracy of infant age per estimation (in days) according to the observation type, i.e. field of photographic observation. The inaccuracy is the absolute number of days between an infant actual and estimated age per observation.